STUDIES ON CELL CONSTANCY IN THE GENUS EORHYNCHUS

BY

HARLEY JONES VAN CLEAVE

B.S. Knox College, 1909; M.S. University of Illinois, 1910

Thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy in Zoology in the Graduate School of the University of Illinois, 1913.

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STUDIES ON CELL CONSTANCY IN THE GENUS EORHYNCHUS[1]

H. J. VAN CLEAVE

From the Zoological Laboratory of the University of Illinois

FORTY-SIX FIGURES

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[1] Contributions from the Zoological Laboratory of the University of Illinois, under the direction of Henry B. Ward, No. 28.

INTRODUCTION

1. Materials

During the fall of 1909 the writer began a study of the morphology of the Acanthocephala under the direction of Prof. Henry B. Ward. It happened that the form first taken up for study, Eorhynchus[2] gracilisentis (Van Cleave), displayed a marked uniformity in the number and arrangement of the nuclei in certain regions of the body. These observations opened the question of how far these phenomena of constancy existed in the other tissues and organs of the body. As additional species in the same genus came to the writer's attention, the analysis was carried on in a comparative manner until at length the present paper deals with the results obtained from the study of five species, namely; Eo. gracilisentis (Van C. 1913), Eo. longirostris (Van C. 1913), Eo. emydis (Leidy 1852), Eo. cylindratus (Van C. 1913), and Eo. tenellus (Van C. 1913). Camera drawings of the probosces (figs. 1, 21, 29, 32 and 35), individual hooks (figs. 2, 30, 33 and 36) and embryos (figs. 3, 24, 34 and 37) of these species, are given in order to show what extreme differences of diagnostic characters may occur even though this study brings out the fact that in many regions of the body each individual nucleus of one species may be homologized directly with a nucleus in a member of a distinctly different species.

2. Cell constancy and its relation to cell lineage

While studies in cell lineage have added invaluable support to the idea of orderliness in vital processes they have failed to carry this idea to its legitimate conclusion. The development of the embryo through the cleavage stages of the ovum to the formation of the germ layers and even up to the beginning of differentiation in the anlagen of the organs of the adult body has been worked out within various species of animals, but most investigators have dropped the problem here. The more or less reg-

[2] The name Eorhynchus has been substituted for Neorhynchus, preoccupied, in a paper now in press.

ular procedure of cleavage and development up to this point has been very generally demonstrated in the forms whose cell lineage has been determined, but it was left for such men as Weismann, Goldschmidt, and Martini to raise the question of a probable further continuation of an orderly process. It was already known that in many instances certain cells are very early set apart for the formation of definite groups of organs or tissues, but no one had actually determined how these organs arise, whether by mere indeterminate continuation of the process of cell division, or in an orderly, specifically predetermined manner. Might not the same forces at work upon and within the embryo during its cleavage stages continue to direct an accurately determined continuation of the cleavage throughout the course of development until the adult form is gained? The works of Goldschmidt and of Martini go a great way toward the confirmation of this hypothesis, at least within certain groups of animals. Their results indicate that in the forms studied mitosis has continued along very definite lines, resulting in a predetermined arrangement of the cellular elements of the adult organs and tissues. In his definition of cell constanc y Martini institutes á comparison, not alone of the numbers of nuclei and their relative positions, but also of the size, shape, and finer structure of the cells, and especially of the staining reactions of the nuclei of the cells.

The writer is surprised to find no reference in the more recent literature on cell constancy to Weismann's exceptionally clear ideas as regards the phenomena of constancy. He writes on this point ('93, p. 59):

> In smaller and simpler organisms each individual cell may well be determined from the germ onward, and not only with the result that the number of cells is a definite one, and the position of each definitely localized: the determination may also have caused individual peculiarities of each cell, in so far as they depend on changes in the germ plasm at all—i.e., are 'blastogenic,'—to appear in the corresponding cell in the next generation.

Such a statement of the fundamental principles underlying the theory of cell constancy coming from such a clear thinker as Weismann, even though at the time unsupported by any mass of

reliable data, is of extreme value in that it forshadows a field of investigation from the viewpoint of the problem of the cytology of heredity before the exact facts in the case have been established.

3. The field of cell constancy

Martini has pointed out concisely the obstacles in the path of an investigation on cell constancy, in his comment upon the difficulty in determining either for or against any such position when extremely complicated relations exist between the component parts of a highly differentiated organ. It would be little less than folly to attempt a study of the cell constancy of an organ in one of the higher animals before the possibilities and the limitations of such a study in some of the simpler forms of life had been determined. As a similar instance, who would have considered the possibility of a regularity in the segmentation of the ovum of a vertebrate, had not the fundamental principles been marked out previously by the pioneers in the field of cell lineage, who chose for investigation such objects as displayed the phenomena of cleavage most clearly and with the least complication? Before going further it may be well to consider the nature of the limitations in the realm of cell constancy. Martini has very justly eliminated the cleavage stages of the ovum from consideration here, for the cells in these stages have not as yet arrived at a condition to which the term cell constancy could be applied properly, for in reality the field is limited to a study of such tissues and organs as have passed through the embryonic stage and are definitely differentiated as physiologically functioning organs. It must be kept in mind that though an organism may under normal conditions have portions displaying absolute constancy, yet in those regions where katabolic and secretory processes are proceeding at such a rate as actually to destroy the tissues, constancy, such as is found in the more stable regions which are practically free from radical metabolic changes, cannot exist. Likewise injury and mutilation of parts of the body with the accompanying excitation to renewed multiplication of cells, may profoundly alter the conditions even though the normal organism might display a

high degree of constancy in the number and the arrangement of its component cells.

Any tissue, the cells of which retain the power of continued multiplication after they have become differentiated, is said to possess the power of physiological regeneration. On the basis of the presence or of the absence of this property, Bizozzero has distinguished three different types of tissues within the human body. Morgan ('01, p. 128) quotes him as follows:

> 1. Tissues made up of cells which multiply throughout life, as the parenchyma cells of those glands which form secretions of a definite morphological nature; the tissues of the testes, marrow; lymph glands, ovaries; the epithelium of certain tubular glands of the digestive tract and the uterus; and the wax glands;
> 2. Tissues which increase in number of their cells till birth, and only for a short time afterward, as the parenchyma of the glands with fluid secretions, the tissues of the liver, kidney, pancreas, thyroid, connective tissue, and cartilage;
> 3. Tissues in which multiplication of cells takes place only at an early embryonic stage, as striated muscle and nerve tissues. In these there is no physiological regeneration.

There is no need of limiting this classification to the tissues of the human body for the general principle applies equally well to the tissues of any animal. The direct dependence of the idea of cell constancy upon the conditions set forth in the second and third groups of this scheme is strikingly evident without the need of further discussion. Those tissues which in most animals possess the power of physiological regeneration have been eliminated or profoundly modified in all forms displaying cell constancy. Two of the most obvious factors involved in accomplishing this reduction of inconstant tissues are modification of organs through degeneration and complete elimination of parts through adaptation to parasitism. Thus in the Acanthocephala adaptation to the parasitic habit has been so complete that all traces of the glands usually associated with the processes of metabolism are wanting. With the elimination of this great group of organs there is presented a condition most favorable for the development of a permanent, fixed, relation of the component parts of the body. In the genus Eorhynchus this finds expression in a surprisingly

marked cell constancy, the evidences of which will be brought out in this paper.

How strict an interpretation is to be placed upon this term 'constancy?' Is the term to be applied with absolute precision, utterly excluding the possibility of variation of any kind, or may some value be placed upon instances in which there is clearly a normal number and arrangement of the cells but in which a few individuals depart from this condition? The former of these two interpretations means the elimination of the possibility of variability and thereby precludes all possibility of evolution, for an absolute constancy could result in nothing else than an absolute fixity of species, since variability is one of the necessary or primary factors in evolution. The question of real importance is how far these phenomena may vary from the normal without entirely invalidating conclusions based upon the varying character in question. It is a very generally accepted fact that the application of stimuli or the action of internal enzymes may give rise to either an acceleration or a suppression of mitosis, thus producing abnormal numbers of cells and resulting in a confusing arrangement of the products. Since endoparasitism leads to a practical elimination of those varying environmental conditions which so profoundly influence the development of the free-living forms, it would be quite natural to look among the endoparasites for materials adapted to the study of cell constancy. Such conditions have been found to exist in members of the genus Eorhynchus.

4. Methods

A method frequently employed in comparing the approximate number of cells in a given organ or region of the body of two individuals consists in making a count of the number of cells present in sections of the two animals at approximately the same plane. Such a method may be sufficient when the problem of relation of cell size to body size alone is being considered, but at best it can form the basis of but the crudest sort of a comparison and is valueless in determining the presence or absence of cell constancy. In order to avoid the possibility of misunderstanding regarding

the accuracy of the results set forth in the following study on cell constancy it should be understood that where a definite number of nuclei is recorded for a given organ that number has been obtained either by careful reconstructions of the part in question or by direct counts of all the nuclei in well cleared toto mounts. In no case has the writer based a strong claim of constancy upon the finding of a similar condition in as small a number as two individuals. In many instances even as high as two hundred individuals of the same species have been studied with the greatest care in order to establish the correctness of a finding.

For general results, killing and fixing in saturated aqueous solution of corrosive sublimate with about one per cent glacial acetic acid were by far the most satisfactory. Dilute aqueous solution of Ehrlich's acid hematoxylin proved best adapted for staining toto mounts. The chief advantage of this technic over all others consists in the remarkable translucence of the object after mounting in balsam. By this method the writer was enabled to study the cytology of even some of the larger forms in toto under a one-twelfth inch oil immersion lens. In the preparation of serial sections the same stain countered with eosin gave good differentiation, but for the finest work iron-hematoxylin was found most reliable.

5. Cell constancy vs. nuclear constancy

Since most of the cell walls in the Acanthocephala have disappeared, the question arises, whether the consideration of such syncitial structures may be included within the bounds of cell constancy or must be considered under an entirely separate heading which might be called nuclear constancy. To the writer the problem finds its solution in the known facts in the embryology of the group. Kaiser has recorded valuable information upon this question of the early development of the Acanthocephala. Regarding the determinate nature of the cleavage in the group he states ('13, p. 5): "Die Entwicklung der Echinorhynchen ist von der ersten Furchung bis zur Ausbildung des definitiven Wurmes völlig determiniert." Most writers have agreed that

the point wherein the Eorhynchi differ most essentially from other Acanthocephala lies in the fact that the nuclei of the mature worms in this genus are derived directly by the differentiation of the embryonic nuclei, while in the other genera there is introduced a period of indeterminate fragmentation of the nuclei at the time of the formation of the adult organs. In view of these facts the writer maintains that the term cell constancy is fully justifiable when dealing with the structure of the Eorhynchi, for each nucleus with the cytoplasm surrounding it represents a cell. Moreover the introduction of a wholly different term in the consideration of phenomena identical with those grouped under the head of cell constancy would but add confusion to the subject, for after all the wall is not the essential part of the cell.

PROOFS OF CELL CONSTANCY IN THE GENUS EORHYNCHUS

1. Cuticula

The cuticula of the Eorhynchi is a thin, homogeneous, layer covering the entire body. Even under a magnification of nine hundred diameters no specialized structure is visible. By virtue of its noncellular structure this body covering is readily eliminated from consideration in this connection.

2. Subcuticula

The subcuticula, which comprises by far the greater part of the body wall (figs. 4, 5 and 23 *s*), lies directly under the cuticula. While the general structure of this tissue in the Eorhynchi closely resembles that of other genera of Acanthocephala, the arrangement of the nuclei is decidedly distinctive of this genus. Another feature wherein these forms vary from their near relatives is that the component layers of the subcuticula are not as clearly defined as in many other genera. O. F. Müller in 1780 (plate 61) figured Eo. rutili (Müll.) and in the body wall showed five 'oscula,' as he called them later (1784), four of them on the dorsal side of the body and a single one on the ventral side near the anterior end. There can be no doubt that these structures are the giant nuclei

of the subcuticula, even though the actual discovery of the nucleus by Brown did not come until half a century later. Even as late a worker as Dujardin ('45) observed the swellings on the exterior of the body caused by these nuclei, though he did not understand their structure and significance. In regard to these same structures in the body of Eorhynchus agilis (Rud.), Dujardin ('45, p. 538) writes: " . . . . strié transversalement et présentant du cote convexe une serie longitudinale de cinq a six grands pores (?) ou disques orbiculaires, et un seule du cote concave; . . . . " In speaking of the same species, Saefftigen ('84, p. 9) refers to four or five subcuticular nuclei in the dorsal canal and two in the ventral canal:

> Bei Ech. clavaeceps haben die Subcuticulakerne einen mächtigen Umfang, ihr grösster Durchmesser übersteigt oft 0.2 mm. . . . . Sie sind bei dieser Species nur in beschränkter Anzahl, ausschliesslich in den Kanälen, und zwar in den Hauptkanälen, deren ganzes Lumen sie einnehmen, vorhanden. Im Dorsalgefäss finden sich ihrer vier bis fünf, im Ventralgefäss zwei, dessgleichen ein bis zwei in jedem Lemniscus.

Linton ('89, p. 490), in describing what he called Echinorhynchus agilis Rud., but was in all probability Eorhynchus cylindratus, notes "large circular spaces in the vascular layer clearly defined by a circular thickened ring of connective tissue." Without further delay he accepts the name 'pores' or 'orbicular discs' introduced by Dujardin, to whose work reference has already been made. However, Linton's data differ from those of Dujardin, as indicated in the following: "In the specimens which I have examined," says Linton, "there does not appear to be either this regularity or proportion in the arrangement, e.g., one specimen had four nuclei on the concave side and two on the convex. In others they could not be made out definitely, but enough could be made out to show they were irregularly placed." However, in justification of modern development of histological methods it would scarcely be proper to leave this statement of Linton's position without noting the fact that his studies were upon living material under a compressor. While it is true that a good preparation of a stained toto mount does display the subcuticular nuclei with remarkable distinctness, yet observations of such nature must

ordinarily be subordinated to those upon carefully prepared serial sections if points of structure are to receive a final analysis.

Hamann ('91, p. 28) refers to the condition of the subcuticular nuclei of Echinorhynchus clavaeceps, now Eorhynchus agilis, in the following terms:

> Das Larvenstadium, in dem die Haut ein Syncytium mit wenigen Riesenkernen bildet, ist bei Echinorhynchus clavaeceps dauernd fixiert. Wie ich in dem systematischen Teil zeigen werde, ist diese Art auf dem Larvenstadium stehen geblieben, was ihre Haut, Muskulatur, Lemnisken anlangt, wir haben einen Fall von Phylo-Paedogenesis vor uns.
>
> Bereits am lebenden Thiere sieht man die 0.2 mm. grossen, eiförmigen bis kugeligen Riesenkerne in der Haut. Ich zählte bei dem in Fig. 1 auf Taf. IX abgebildeten männlichen Tiere acht Kerne in der Epidermis und je zwei in den Lemnisken.

It is interesting to observe that the foregoing statement as to the number of nuclei is not put in general form but only indicates that one individual possessed eight subcuticular nuclei. As the result of the examination of several hundred individuals of the genus Eorhynchus the writer has found but a single one in which the arrangement and number of nuclei varied from the typical condition of one ventral and five dorsal subcuticular nuclei. This, in itself, would seem to indicate the the specimen which Hamann was describing was abnormal. Lühe ('04, p. 294), commenting upon the works of Müller and Hamann regarding the nuclei of the subcuticula, writes: "In der Figur Hamann's sind freilich 6 Kerne in der Haut gezeichnet. Aber wenn die Zahl dieser Kerne auch innerhalb gewisser Grenzen schwankt, so habe ich doch gerade die von O. F. Müller gezeichnete Fünfzahl verhältnismässig häufig beobachtet und alsdann auch stets in der von Müller gezeichneten Anordnung."

These records, while of importance historically, cannot be regarded as infallible, primarily because in each case they were made in the form of incidental observations rather than as accurate determinations. The following paragraphs present the results of my studies on subcuticular nuclei of five American species.

Eorhynchus gracilisentis. In this species the nuclei of the subcuticula conform to so distinct a pattern, as regards numbers and

arrangement, that variation beyond that which is capable of explanation on the basis of the degree of contraction is limited to a single instance. Each one of more than two hundred individuals had six nuclei in the subcuticula, arranged according to the following system: Five large nuclei occupy positions in the mid-dorsal line of the body. Three of these constitute a group toward the posterior end of the body while the remaining two are separated slightly farther from the rest and lie anterior to the group of three, but are included in the same sagittal plane as the posterior nuclei. In sexually mature individuals these nuclei averaged 0.078 mm. by 0.045 mm. The sixth nucleus of the subcuticula is located in the mid-ventral line, near the anterior end of the body, usually at a point between the anterior and posterior groups of the dorsal series. It is more elongated and larger than the other nuclei of this tissue, having a long axis of 0.125 mm. and a smaller diameter of 0.050 mm. These nuclei are irregularly ovoid in shape, though occasionally they are reniform as shown in figure 4, *sn.5*. The chromatin usually has a closely compacted arrangement, but sometimes takes the form of an irregularly branching network within the nucleus. The shape of the nuclei in this tissue of the Eorhynchi is in decided contrast to that described by Graybill ('02) for the nuclei of the subcuticula of Echinorhynchus thecatus Linton. According to that writer the nuclei of this last named species are of a wonderfully dendritic nature, each having a broad expanse of finely branching processes. The contrast is none the less striking if a comparison be made with the subcuticular nuclei of any other type of Acanthocephala. Three types of subcuticular nuclei are thus distinguishable in the Acanthocephala; the giant nuclei of the Eorhynchi, the dendritic nuclei of E. thecatus, and the numerous small nuclei scattered throughout the subcuticula as in most other Echinorhynchi and some of the other genera.

Only one specimen of all the Eorhynchi examined showed variation in the number and arrangement of these nuclei such as might be expected, judging from the statement of previous investigators. This individual was a small, immature female. Even here the variation was purely one of arrangement of the com-

ponent nuclei, for numerical constancy remained undisturbed. In this case one nucleus normally in the anterior dorsal group had taken a position on the ventral side of the body. Before trying to explain this departure from the normal, attention must be called to the following points:

1. The nuclei in the dorsal line lie within the dorsal longitudinal canal, and the one nucleus on the ventral side of the body is similarly situated in the ventral canal. These two canals communicate directly through the circular canals of the lacunar system.

2. Hamann ('91, p. 21) ascribes to the nuclei of an Echinorhynchus in the embryonic state the power of amoeboid movement.

3. Since it is a well-known fact that some nuclei may wander to that part of the cell where they can best perform their functions, and may even penetrate heavy cell walls in order to reach a distant point of injury; may not the displacement of the nucleus in the abnormal specimen of Eorhynchus gracilisentis just cited be explained as the result of either active amoeboid movements which carried it along the lacunae to the opposite side of the body, or as a migration of the nucleus brought about by some local irritation or injury of the body on the ventral side?

In no other instance has the writer seen the parallel of Lühe's figure of Eo. rutili (copied as fig. 31) in which he portrays four dorsal and two ventral subcuticular nuclei (Lühe '11, p. 12, fig. 1).

Eorhynchus longirostris. The nuclei of the subcuticula of this species differ but little from those of the preceding species. In the first place the median dorsal row of five nuclei is not so clearly divided into an anterior group of two and a posterior group of three nuclei. The nuclei of this region are almost equidistant one from another. Moreover the terminal member of this series approaches nearer to the posterior tip of the body than does the terminal nucleus in Eo. gracilisentis. The swellings upon the surface of the body caused by the presence of these nuclei are more distinct in toto mounts of Eo. longirostis than in mounts of the preceding species. The dorsal nuclei have as an average, a long

diameter of 0.132 mm. and a short axis of 0.048 mm. while the ventral nucleus ranges in size near 0.250 × 0.057 mm. Instead of occupying a position posterior to the second dorsal nucleus, as in Eo. gracilisentis, the ventral nucleus of this species is typically opposite the foremost of the dorsal series. A slight variation does occur with regard to the relative location of the ventral nucleus but this probably is due to difference in degree of contraction of various individuals.

Eorhynchus emydis. Though the individuals of this species are very much larger than those of either of the preceding species, being from 3 to 32 mm. long, yet the number of nuclei in the subcuticula is the same. Using the arrangement of the nuclei of the subcuticula as a basis for argument it appears that the excessive size of the species is brought about by an elongation of the posterior region of the body rather than by a uniformly distributed elongation. The evidence for this lies in the fact that, while the two anterior dorsal nuclei remain relatively close together, the three of the remaining group are separated from each other by a marked interval. The ventral nucleus occupies a position opposite that of the foremost of the dorsal row, or, occasionally, a little anterior to it. No variations of number or of arrangement were observed in the numerous individuals of this species which were studied.

Eorhynchus cylindratus. Here, again, is found the typical number of subcuticular nuclei. The distribution of the dorsal nuclei closely approaches that found in Eorhynchus emydis (Leidy), but the ventral nucleus more often takes a position midway between the two anterior dorsals, approaching nearer to the posterior of these than to the anterior as in Eo. emydis. The distribution of the dorsals strongly suggests that found in the preceding species.

Eorhynchus tenellus. In this species, likewise, the five dorsal nuclei and one ventral nucleus in the subcuticula have an arrangement similar to that of Eo. emydis.

3. Lemnisci

These unique structures, while extremely simple in organization, have been the subject of considerable speculation among writers dealing with the genus Eorhynchus. Saefftigen ('84, p. 9) recorded two nuclei in each lemniscus of Eo. rutili (Müll.). Hamann ('91, p. 140) corroborated this for the same species and later ('95, p. 30), described the same condition for the only other then known species of the genus, Eo. agilis (Rud.). He mentioned an instance of an immature form of Eo. rutili in which only one nucleus was present in each lemniscus, while the second nucleus was just in the process of formation. He says, "Ein junger Echinorhynchus clavaeceps, der mir vorliegt, zeigt gering entwickelte Lemnisken, die aber bereits den einen Kern enthalten, während der andere noch an der Grenze ihrer Entstehung liegt." This condition finds ready explanation in the light of facts brought out later in this article. Still more recently Lühe ('11, p. 12) recorded two nuclei in each lemniscus of Eo. rutili. His figure 1, copied here as figure 31, shows but a single nucleus in each lemniscus.

It seems hardly necessary to mention that these observations as given by various writers on the Acanthocephala add nothing to the direct evidence for or against the problem of cell constancy. However, they do serve to indicate the ease with which one may be led to accept the assertion of an earlier worker without fully following out the evidence upon which his statements are founded. To one working on a purely anatomical problem it is extremely plausible to decide that a form is immature when only a single nucleus appears where others say two should occur. Such seems to have been the condition when Hamann reported this abnormality, but, in the light of the present study of the structure of the lemnisci of the numerous examples of Eorhynchi, it is difficult to see the source of this evidence of a second nucleus just at the beginning of its formation. All the facts gained from the study of five species of this genus point to a condition mentioned by none of these previous investigators, namely, while one lemniscus possesses the two nuclei so generally ascribed to each, the other

in no case has more than a single one. Figures 22 and 43 indicate clearly this relation of the nuclei in the lemnisci.

An obvious explanation of the cause of so many investigators going astray on the question of the number of nuclei in the lemnisci is found in the generally accepted conclusion that these are paired lateral organs. Therefore as soon as two nuclei were demonstrated in one of them it was the natural thing to expect a duplication of this condition in the organ of the other side of the body. Failure to recognize both nuclei in each of the two lemnisci could be accounted for by the interference of overlying parts. Or even in case serial sections were examined in this connection the lemnisci are usually so much twisted and coiled about one another that, unless reconstruction drawings are made, one is not sure of the interpretation of the numbers and relationships of the nuclei.

Eorhynchus gracilisentis. The small size of the lemnisci in this species, and the fact that their usual condition is a mass of twists and turns in the anterior end of the body, together serve to render an accurate analysis of the exact structure very perplexing. The careful study of serial sections of numerous individuals fully demonstrated the inequality of the two organs. Invariably one lemniscus was found to be supplied with two large nuclei lying in the axis of the canal, while the other contained but a single nucleus in its canal. These nuclei so closely resemble those of the subcuticula that no special description seems necessary for them. In shape they are more elongated and display more of a tendency toward a pointed condition at either end.

Eorhynchus longirostris. In this species the lemnisci demonstrate the point in question most admirably (fig. 22). Here reconstructions from serial sections were needless, since the nature of the lemnisci was such that each stood out as a distinct, practically straight tube extending backward into the body cavity. An examination of toto mounts was sufficient to demonstrate that one of these organs possessed two nuclei of the subcuticular type while the other had but a single nucleus.

Eorhynchus emydis. It was from the study of the whole mounts of immature forms of this species that the writer first

gained the correct conception of structure of these organs, which has been carried in a comparative way to the other members of the genus. In these sexually immature stages the lemnisci appear as a pair of small sac-like projections into the anterior end of the body cavity, and in these sacs the nuclei are readily distinguished. It might be argued that as sexual maturity is reached changes occur in the structure of the body, resulting in either an increase in the number of the nuclei or a redistribution of them. Hence the study of these juvenile forms was supplemented by careful observations on the condition in fully mature individuals. These entirely confirm the results obtained for the much smaller, sexually immature members of the species. Figure 43 indicates the absolute clearness with which the nuclei appear in these organs.

Eorhynchus cylindratus from the black bass, Micropterus salmoides (Lacépède) has much longer lemnisci than the preceding species but the arrangement and number of its nuclei are identical with the conditions described for each of the preceding species of Eorhynchus.

Eorhynchus tenellus. Here again the same condition is met in the nuclei of these organs.

Hamann ('95, p. 9) said: "Die Lemnisken sind als Fortsetzung der Haut der Körperwand anzusehen." In all the foregoing species the nuclei of the lemnisci so closely resemble those of the subcuticula in structure that this fact might well be used as an argument in support of the view that these organs arise as inpocketings of the body-wall. Moreover, the fact that their position in the canal of each lemniscus corresponds to the condition found in the subcuticula where the nuclei also occur in the longitudinal canals of the body, indicates a possible connection or relationship between these two sets of canals. No direct connection, however, has been made out by the writer in members of this genus, although such a connection is rather easily demonstrated in members of other genera of Acanthocephala.

One rather common variation in the form of the nuclei of this region of the body consists in the tendency to assume a rounded outline in immature forms as contrasted with the more elon-

gated and less regular outline of each nucleus in the fully mature animal. At the same time this variation in shape is accompanied by just as striking a difference in the manner in which the chromatin material is distributed. While in the adult the chromatic substance is arranged in a more or less irregular branching figure in the midst of the nucleus, in the immature condition the chromatin is more evenly distributed throughout the nuclear mass.

4. Proboscis and proboscis receptacle

While ordinarily the proboscis and its receptacle are considered as two separate organs or regions in the Acanthocephala, in the following it seems better to consider the two together, since certain structures are not limited to either but extend through both. Even though the proboscis shows practically no individual variation within the species, yet the different species may vary to a remarkable degree. On the other hand, several species of this genus present such slight variation in this organ of attachment that the only evident point of contrast is in the relative size of the various rows of hooks. In spite of the considerable range of shapes and structures in different species, the following analysis will show that in all probability the same nuclei contributed to the formation of structures which are distinctly different in one group from those found in closely allied species of the same genus. In other words, it seems that during the processes of differentiation variations may have occurred in the resulting structures but that the cellular elements entering into the differentation were the same in number in each species.

At the tip of the proboscis (figs. 6 and 38 *po.*) is a structure of questionable function and of variable form within the genus. This structure, which occupies the central region of the proboscis, is, in some species, an elongated cylindrical sac while in others it more nearly approaches a globular form. Various functions have been ascribed to this peculiar mass of tissue. Lespes ('64) considered a similar structure in Echinorhynchus clavaeceps as the indication of an alimentary canal. Of a similarly located structure made up of two cells in E. proteus Baltzer ('80, p. 26)

made the statement "Wahrscheinlich stehen diese Zellen mit einem, hier vorhandenen Tastvermögen in Beziehung." Saefftigen ('84) thought this condition in E. clavaeceps resulted from the four retractors of the proboscis forming a space between them and in this the nuclei had come to lie.

Hamann ('91, p. 51) has shown that in the ontogeny of E. proteus a group of three cells is laid down at the anterior end of the proboscis early in development. "An der Spitze sind auf dem Schnitt drei der grossen Kerne mit ihrem kugeligen Kernkörperchen getroffen, deren Zellsubstanz den centralen Teil der Rüsselanlage bildet," He has found such cells in all species of Echinorhynchus which he has investigated. As to their location and relations he adds ('91, p. 57): "Bei Echinorhynchus proteus und angustatus liegen sie nebeneinander, bei Ech. clavaeceps hintereinander . . . . Seine Abbildungen lassen das Verhältnis dieser Zellen zur Haut (Subcuticula) nicht deutlich erkennen." Hamann considers the evidence insufficient to warrant the naming of this structure an alimentary tract. On the other hand he has offered the suggestion that the staining reaction of this tissue in E. clavaeceps is such that the granular structure with hematoxylin staining indicates a glandular function. For this reason he called the cells gland-cells. I do not consider the evidence sufficient to warrant ascribing a definite glandular function to this structure, but since there does not seem to be any close relationship between it and the other organs, might it not be the vestige of some organ which through disuse has degenerated since the Acanthocephala have acquired the parasitic habit?

Eorhynchus gracilisentis. This terminal organ of the proboscis in Eo. gracilisentis (fig. 6). contains three large oval nuclei lying in its long axis. It will be recalled that this arrangement of the nuclei is what Hamann ('91, p. 57) has described for Eo. rutili. The relative position of these is apparently influenced by the state of contraction of the proboscis muscles. In case the proboscis is fully extended these nuclei assume a regular oval form, the long axis of each coinciding with the long axis of the body, but in various stages of contraction of the proboscis these nuclei become slightly modified in their relations. When forced closer together, they, at times, come to lie with their long axes at right angles to the main

axis of the body. However it does not seem necessary to do more than mention that this abnormal or unnatural position is simply the result of the action of an external physical force and for this reason would not come under the consideration of abnormalities of location such as were discussed under the nuclei of the subcuticula.

A dense chromatin mass lies in the center of each of these nuclei. This mass at times is distinctly oval, again it may be irregularly branched, and finally it frequently appears as several smaller rounded masses scattered throughout the nucleus. In this same species a pair of small nuclei occurs in a clearly demarked area at the base of the terminal organ of the proboscis. These are usually almost perfectly spherical, but at times they assume a slightly ovoid shape (fig. 7).

Eorhynchus longirostris. In this species (figs. 22 and 26, *po*) the nuclei of the terminal proboscis organ have the same number and arrangement as just described for Eo. gracilisentis.

Eorhynchus emydis (Leidy). This form possesses a terminal proboscis organ of the type described by Hamann for E. proteus and E. angustatus. It is supplied with two large oval nuclei in the central enlarged portion and with two small spherical nuclei in a region at their posterior margin. The general relations of these parts are well shown in figure 45, a copy of Hamann's figure 28, plate 3, representing the condition found in Eo. agilis (Rud.).

Eorhynchus cylindratus. The terminal organ of the proboscis has the same structure and arrangement of nuclei as emydis. The two large oval nuclei lie side by side, while the two smaller ones occur posterior to them.

Eorhynchus tenellus. Here the organ at the end of the proboscis (fig. 38, *po*) is of the type just described for the last two species, and the constancy of the cellular elements is identical.

5. Proboscis wall and receptacle wall

Eorhynchus gracilisentis. The nuclei of the walls of the proboscis and its receptacle in this species have the following arrangement: The anterior end of the proboscis bears a circle of twelve nuclei, located in the region near the bases of the terminal hooks,

yet no direct connection could be traced between nuclei and hooks. Figure 10 shows the relations of these nuclei in a cross section of the proboscis. The nuclei of this group are small spheres of chromatin 0.005 mm. in diameter, each lying in the center of a 0.007 mm. clear space. Two pairs of nuclei are connected with the muscle sheath which effects the retraction of the hooks. These lie, one on the dorsal side of the proboscis and one on the ventral side, in the region between the second and basal rows of hooks. The location of these nuclei is shown in figure 6, which is a single sagittal section including but one nucleus of each of the two pairs.

The muscular wall of the proboscis receptacle proper has three pairs of nuclei. The most conspicuous of these is a pair of oval nuclei connected with the sheath musculature directly at the base of the brain (fig. 8). The other two pairs are located, one pair dorsally and the other ventrally, on the wall of the receptacle just anterior to the brain.

Eorhynchus longirostris. Due to the crowded condition of the receptacle in this species, brought about by the usual partial inversion of the proboscis, very little could be made out regarding the cellular structure of the proboscis receptacle. The two nuclei associated with the muscular wall at the base of the brain are very distinct.

Eorhynchus emydis. The muscular wall of the proboscis re-receptacle is supplied with three pairs of oval nuclei. One pair is located on the inner wall of the receptacle at the base of the brain. The other two pairs are located on the inner side of the dorsal and ventral walls, a short distance cephalad from the brain. In the proboscis two pairs occur, one on the dorsal side of the proboscis wall and the other pair on the ventral, in the region of the bases of the middle row of hooks.

Eorhynchus cylindratus presents a nuclear constitution of the proboscis and its receptacle identical with that of Eorhynchus emydis.

Eorhynchus tenellus has the same arrangement of the muscular nuclei in the proboscis sheath and proboscis as the two preceding

species. This arrangement is shown in figure 38, from which one nucleus of each pair of dorsal and ventral receptacle wall nuclei has been omitted in the reconstruction.

6. Invertors of the proboscis

Eorhynchus gracilisentis. The proboscis invertors consist of two strips of tissue which extend backward along the dorsal and ventral surfaces of the terminal proboscis organ and pass through the base of the proboscis sheath. In the region anterior to the brain each invertor bears a pair of elongated or spindle shaped nuclei. In this species the invertors are so highly developed that they almost entirely fill the space within the walls of the proboscis and its sheath.

Eorhynchus longirostris. In this species the same structures are found. The invertors are somewhat reduced in size so that they stand out more clearly as separate structures. As in the preceding case each of them is supplied with two nuclei. Figure 26 shows these invertors cut in a slightly diagonal plane so that but a single nucleus shows in each.

Eorhynchus emydis. Figure 44 is a drawing from a toto mount showing the pair of nuclei associated with each invertor.

Eorhynchus cylindratus. The nuclei in the invertors are identical with those found in Eo. emydis. The invertors are in about the same stage of development.

Eorhynchus tenellus presents the same distribution of one pair of nuclei to each invertor, as shown in figure 38.

7. Retractors of the proboscis receptacle

In the genus Eorhynchus the retraction of the proboscis receptacle is accomplished through the contraction of two long fibrous bands which proceed from the posterior end of the proboscis receptacle and find attachment, one on the dorsal wall of the body and the other on the ventral body-wall. These retractors are direct continuations of the proboscis invertors.

Eorhynchus gracilisentis. The dorsal retractor of the proboscis receptacle in this species is supplied with two oval or spindle

shaped nuclei whose arrangement is shown in figure 16. The ventral retractor of this same species is similarly furnished with two nuclei. These are of the same type as those already described for the dorsal retractor. In no case was any evidence discovered indicating the presence of other nuclei of any type in these structures.

Eorhynchus longirostris. In members of this species the arrangement of the proboscis receptacle retractors is identical with that just set forth for Eo. gracilisentis. The nuclei are of the same number, the same appearance, and have identical relations within the retractors. Figure 28 shows the nuclei of the dorsal retractor of the proboscis receptacle.

Eorhynchus emydis (Leidy), Eorhynchus cylindratus, and Eorhynchus tenellus show the identical condition of the retractors of the receptacle as described for the other species of the genus.

8. Cement gland

In members of the genus Eorhynchus the cement gland presents a condition at wide variance from the type most commonly found in the other genera of Acanthocephala. Instead of consisting of a series of independent sac-like glands in the posterior region of the male, as in many genera, the cement gland is a compact mass. Bieler ('13) has suggested that this deviation in structure, together with the fact that a single covering encases the mass, is of value in differentiating the Eorhynchi from their near relatives. This characteristic was not mentioned by Hamann in his definition of the genus. In all of the species examined the nuclei of the cement gland are oval with a compact central chromatin mass.

Eorhynchus gracilisentis. In this species eight large oval nuclei lie imbedded in the mass of the gland (fig. 9, *cg.*) These are the only nuclei present in the entire structure. The study of toto mounts and of sagittal sections demonstrated that, though these nuclei are uniformly distributed through the gland, there is an evident arrangement in two lateral groups each of four nuclei.

Eorhynchus longirostris. The gland in this species stands in marked contrast to the type preceding. While the nuclei are clearly of the same character as those of Eo. gracilisentis their number is just doubled. Instead of the eight large oval nuclei there are sixteen of the same general character (fig. 20, *cg*).

Eorhynchus emydis. This species contains a long cylindrical cement gland bearing eight nuclei. The size of the gland is indicative of the degree of maturity of the individual. Figure 42 shows this gland in an immature male. The eight nuclei within this small mass are arranged in two distinct groups. The same gland in a fully matured worm not only has increased considerably in size (fig. 41) but at the same time has undergone a complete rearrangement of the component nuclei, resulting in a single line of nuclei running the length of the gland.

Eorhynchus cylindratus and Eorhynchus tenellus both have cement glands of the type just described. In each case the eight large nuclei occur in an elongated cylindrical organ. The arrangement of the nuclei in each of these species is the same as that described for Eo. emydis.

9. The male genital apparatus

Eorhynchus gracilisentis. The cirrus in this form is supplied with nuclei of two types, and in some instances a clear distinction could be drawn between the two kinds of tissues connected with the respective types of nuclei. The portion of the cirrus lying nearest to the sperm duct has a pair of large lateral nuclei in the dorsal region (fig. 18, *ci*) in which the chromatin has a strikingly characteristic arrangement in small masses scattered through the nucleus, with a tendency toward collecting on the nuclear wall. These spheroidal nuclei are 0.007 mm. in diameter. Slightly anterior to this pair of nuclei and in the region of the cirrus farthest removed from the duct are two slightly larger spherical nuclei (fig. 18, *ci*) measuring about 0.009 mm. In these the chromatin tends toward the formation of closely compacted masses lying in the center of the nuclei.

The walls forming the vas deferens have two nuclei just ventral to the cement gland. These nuclei have a diameter of 0.007 mm., and each contains a single chromatin mass 0.003 mm. in diameter. A slight ventral dilation of the vas deferens in that part of its course just opposite the posterior edge of the cement gland where it enters the sperm reservoir, is supplied with two small nuclei. These are bilateral in arrangement. Each has a long axis of 0.005 mm., and a short axis of 0.003 mm.

The muscular sac posterior to the reservoir of the cement gland contains two star-shaped nuclei which lie close to the anterior end of this structure. These have the appearance of lying in a very loose mass of tissue, sending out small projections to the more solid surrounding portions of the sac wall. The muscular wall of this sac contains a small pair of nuclei on its dorsal surface near the posterior end. These are of the type of small oval nuclei found in the body musculature of this genus. Figure 17, *ms*, shows the relations of this structure as presented in a reconstruction from sagittal sections. Very similar conditions have been found in the other species of Eorhynchus but the study has not been carried out in detail. Figure 25 indicates the appearance of the pair of nuclei within the muscular sac of Eo. longirostris.

The inturned portion of the posterior region of the male, extending from the exterior to the cirrus, is curiously modified in the region nearest the genital opening when the copulatory apparatus is retracted. At this place there are formed a series of five closely fitted wedge-shaped structures, each of which bears three nuclei, as shown in figure 18, which is a reconstruction drawing from serial sagittal sections. The same condition has been demonstrated in well cleared toto mounts of this species. Connecting this structure surrounding the genital orifice with the arms of the copulatory bursa there is an extremely irregular, inconstant portion , the walls of which vary so in appearance with the various states of retraction or of protrusion of the genital apparatus that the writer has not been able to establish a definite number or arrangement of the nuclei contained in it (fig. 18).

10. The female genital apparatus

Eorhynchus gracilisentis. The vagina presents a clear example of constancy of number and arrangement of the nuclei. Four large nuclei (figs. 11, 12 and 13, *v*) are found in its inner muscular layer between the genital orifice and the sphincter vaginae. Two nuclei are associated with the sphincter. The outer non-muscular layer of the vagina in the region of the sphincter contains three nuclei. Cephalad from the sphincter the vagina has a short rounded region consisting of a thick walled tube through which the embryos must pass from the uterus into the orifice of the sphincter. This heavy walled portion of the vagina bears four large nuclei. Anteriorly, the outer wall of the vagina passes over into the single-walled uterus with its large sac-like cavity. On the dorsal side of the uterus at its junction with the vagina there is an enlargement of the wall in which are found two nuclei, the only ones associated with the uterus. Figures 11, 12 and 13, *u*, *v*, and *vs*, show the relations of these parts, together with a representation of the nuclei. The selective apparatus (fig. 11, *sa*), because of its extremely complicated structure, gives considerable trouble when an attempt is made to compare the nuclei of one individual with those of another. The eight nuclei shown in the drawing just cited have been found in every individual studied, but several other nuclei which occurred in this region in some individuals could not be found in others of the same species. The hard shelled embryos with which the body of a mature female is filled hide this structure almost completely in toto mounts, and in serial sections the embryos frequently cause it to be so torn that very little of the actual relations may be made out. Extending posteriad from the dorsal wall of this selective apparatus are two muscular strips whose function is evidently to support these organs since each finds a point of attachment on the dorsal wall of the body. One nucleus occurs in each of these (fig. 11, *ssa*). On either side of the genital orifice of the female there extends a broad fan shaped ligament which becomes attached to the dorsal wall of the body cavity (fig. 15, *fl*). In the broad portion

near the genital orifice each ligament contains a single large star-shaped nucleus.

Eorhynchus longirostris. In this form the vagina, from the genital orifice to the sphincter, is supplied with four nuclei, as shown in figure 27. The two nuclei associated with the sphincter, which can be made out clearly in serial sections, are not shown in this drawing. Anterior to the sphincter are four vaginal nuclei. The uterus, as in all other species studied, has but two nuclei and these occur at its posterior extremity. As a consequence of the difficulties involved in studying the selective apparatus, as pointed out above, the writer has been unable to establish any definite results regarding the occurence of nuclei in that organ.

Eorhynchus emydis. In immature individuals of this species the female tract presents a very diagrammatic arrangement of the component structures. Figure 40 shows the nuclei with which the vagina below the sphincter is supplied. These four nuclei are arranged in pairs, one at either end of the region. The sphincter muscle has a single pair of nuclei. Anterior to the sphincter the thick walled portion of the vagina has four nuclei arranged in two pairs as shown for Eo. gracilisentis. The uterus has a single pair of nuclei at its posterior extremity. In the selective apparatus six pairs of nuclei could be seen distinctly. Of the two muscles (fig. 40, *ssa*) for the support of this organ each bears a single nucleus.

Eorhynchus tenellus. Reference to the figure will show that the female genital tract of this species (fig. 39) bears identically the same nuclei as have been described for Eo. emydis.

11. The brain

Eorhynchus gracilisentis. In the brain of Eorhynchus conditions are such as to render a careful analysis of the structure difficult. This organ (fig. 8, *br.*) is a conical mass of ganglion cells having an extreme length of 0.1 mm. The cells of which this mass is composed are small rounded bodies of uniform character so that there are no regions demarcated by variations in the size or structure of the component cells. The small, 0.005 mm., cells

are so closely packed together that even in a most careful reconstruction from thin serial sections one is never absolutely certain that in some cases two adjoining sections do not contain parts of the same nucleus. Reconstructions of two individuals from drawings of serial sections magnified nine hundred diameters gave in one instance one hundred and eight cells in the brain, in the other one hundred and nine. While these facts are not given with the idea of establishing an absolute constancy they may be taken to indicate that, even though the structure in this region is so extremely crowded, yet there is a close agreement in the results obtained from these two reconstructions.

Eorhynchus emydis. A reconstruction of the brain of a single individual of this species gave ninety-four nuclei as the total for that structure.

12. The genital ganglion

Eorhynchus gracilisentis. Eighteen cells are grouped together in the region of the cirrus in the male to form what is commonly spoken of as the genital ganglion (fig. 17 *gg*). As in the brain, these cells are all of the same type, giving no basis for a division of the ganglion into regions according to the structure of the component elements.

13. Body musculature

Eorhynchus gracilisentis. Two reconstructions of the body musculature each gave a total of thirty nuclei associated with that tissue. These were arranged in fifteen pairs, extending from the union of the body with the proboscis, caudad to the posterior extremity, one nucleus of each pair having a position slightly lateral to the dorsal canal. The distribution is such that a single cross section could not contain more than a single pair of nuclei. The difficulties involved in the determination of the number of nuclei present in this tissue consist chiefly in the discrimination between these nuclei and the embryos, which, in the female, are often so closely packed against the wall that only the most careful study will reveal whether a given structure is associated with the muscle layer or merely closely applied to it. The position of these nuclei in longitudinal section is shown in figure 5.

SUMMARY OF CELL CONSTANCY IN THE GENUS EORHYNCHUS, WITH TABLE OF RESULTS

Consideration of the facts presented in the foregoing parts of this study has led the writer to a firm belief in a remarkable degree of constancy in all the somatic structures in the genus Eorhynchus. Failure to demonstrate this beyond a doubt for all the organs is due to physical limitations, primarily, rather than to conflicting data, for in every instance where a positive count has been made under conditions precluding the possibility of error in manipulation, the same number and arrangement of the nuclei has been found in every individual of the same species. Table 1 summarizes the results found for the five species studied.

TABLE 1

ORGAN OR TISSUE	EO. GRACILISENTIS	EO. LONGIROSTRIS	EO. EMYDIS	EO. CYLINDRATUS	EO. TENELLUS
Subcuticula	6	6	6	6	6
Terminal proboscis ring of nuclei	12				
Terminal proboscis organ	5	5	4	4	4
Leminisci, 1 and 2	3	3	3	3	3
Retractors of hooks	4		4	4	4
Wall of proboscis-receptacle	6	2+	6	6	6
Proboscis invertors	4	4	4	4	4
Proboscis sheath retractors:					
Dorsal	2	2	2	2	2
Ventral	2	2	2	2	2
Cement gland	8	16	8	8	8
Cirrus	4				
Vas deferens	2				
Muscle sac:					
Inside	2				
Wall	2				
Inverted part of male (posterior)	15				
Vagina	11	8	8	8	8
Uterus	2	2	2	2	2
Vaginal sphincter	2	2	2		2
Selective apparatus	8+	?	12		12
Stays of selective apparatus	2	2	2		2
Ligaments at orifice of female	2				
Brain	108 (?)		94 (?)		
Genital ganglion	18				
Body musculature	30				

GENERAL PROBLEMS RELATING TO CELL CONSTANCY

1. Cell size vs. body size

A problem such as the relationship existing between body size and cell size is often approached only from a teleological point of view. Given as the end result the adult body form, that becomes the goal toward which the development of the organism is directed. Thus the possibility that this final body form and size may be a mere incidental result attained through precisely determined series of processes of development is entirely ignored. In other words, a common conception of body form and size might be crudely expressed in the idea that nature establishes a mold for each particular type of body form and that, given a zygote of a definite size, the development of the individual must consist in attaining the boundaries of size and form set for that species, regardless of the number of cell divisions that may be required for that purpose. According to this interpretation, the size of the body is the constant factor while the number of cells which go to make up the organism is purely a matter of circumstance.

The problem of the origin of the adult body and the relationship between body size and size of the component cells is one of long standing. While the following discussion does not attempt to bring all the literature upon the subject into relationship, it will serve to give some idea of the nature of the contentions on the various sides of the problem. Conklin is one of the staunch supporters of the view that not only is cell size fixed but also that it bears no direct relation to body size. In Crepidula fornicata, in which large and small individuals occur, he has shown ('98) that the difference is due entirely to the larger number of cells in the larger individuals:

> In Crepidula therefore the cell size is constant, and variations in the size of the body are due to variations in the number of cells present. The dwarfs are what they are by reason of external conditions and not because of inheritance; they are in short a physiological and not a morphological variety. In such a case the shape and size of the body as well as the number of cells in the entire organism, are greatly modified by the direct action of the environment.

A general presentation of the recent results upon the relations between body size and cell size is given by Minot ('98, p. 65):

> Cells do not differ greatly from one another in size. The range of their dimensions is very limited. This is particularly true of the cells of any given animal. Recent careful investigations have been made upon the relation of the size of cells to the size of the animals, and it has been found that animals are not larger, one than another, because their cells are larger, but because they have more of them. . . . . For example, a large frog differs from a small frog or a large dog from a small dog by the number of cells.

To the writer the foregoing statement has the appearance of too strong a generalization from a limited group of facts. In reality the cells of some animals do differ greatly from one another. Thus in Eorhynchus emydis, while the adult body form is perfectly presented in a small individual 1.7 mm. long, the maximum length of this species is over 30 mm., and both of these individuals have identically the same number of somatic cells. Even a most conservative calculation of the relative size of the subcuticular cells of the small and the large individuals shows that their ratio based on volume is 1:140. Since the subcuticula is a syncytium, this calculation is based on the ratio of the volumes of the subcuticula in the two individuals. The volume is determined by taking the product of the length, by the circumference, by the thickness of the subcuticula. Since the number of nuclei present in the small and the large individuals is the same, the ratio of the volumes of the entire subcuticula of the two individuals is the same as the ratio of the individual cells composing it. It would seem that the range of their dimensions in this case is *not* very limited.

Closely associated with this problem of cell size and body size, and growing directly out of it, is the question of the relation between the number of cells present in the organs of the different individuals. In the analysis of any given organ four possibilities of this relation exist: (1) Body size and cell size are both fixed. Of necessity in this instance the number of cells is just as sharply fixed. No case of this sort is known to the writer; (2) Size of the cells is fixed but the body size may vary. Conk-

lin's results on Crepidula exemplify this condition. The number of cells in any given organ may consequently vary within undetermined limits; (3) Body size is fixed while the size of the component cells may vary. There could be no precise limit to the number of cells in this instance; (4) Body size and cell size may both vary. This last possibility is still further divisible into two conditions: (a) if cell size and body size vary independently no necessary connection exists between the size of the body and the number of component cells, while (b) if body size varies directly as the size of the cell the number of cells in any given organ becomes a fixed quantity, as in the case outlined under (1). It is in accordance with the last possibility that the explanation of the condition found in the genus Eorhynchus is to be sought. In general it is in organisms having this fixed correlation between body size and cell size that cell constancy is to be found.

Regarding the cell lineage of Nereis, Wilson ('92, p. 377) writes: "The entire ontogeny gives the impression of a strictly ordered and predetermined series of events, in which every cell division plays a definite role and has a fixed relation to all that precedes and follows it." How readily this conception of ontogeny lends a support to the theory of cell constancy. In another connection, Wilson, ('00, p. 390) has stated that the number of cells produced for the foundation of certain structures is often fixed. For example, in annelids and gasteropods "the entire ectoblast arises from twelve micromeres segmented off in three successive quartets of micromeres from the blastomeres of the four-cell stage."

By way of explanation of this condition as indicated by Wilson and by Morgan, two possibilities present themselves, either (1) a constancy in numbers of cellular elements is the primitive condition of development which, as Conklin points out, is retained only in the early stages of ontogeny of the metazoa, or (2) cell constancy is a manifestation of a tendency toward fixity which is acquired only at a late stage in the development of a race.

That there is a tendency for the same number of embryonic cells to be used in the formation of the organs and structures of

the body is evidenced by the results obtained by Morgan in his experiments upon the embryos developed from isolated blastomeres of echinoderms and of chordates. In 1896 he found that the larvae of Amphioxus developed from isolated blastomeres of the two and four cell stages tend to utilize the same number of cells for the formation of the organs of the body as do the normal larvae. In the formation of the gastrula stage the normal larvae invaginate about one-tenth of the total number of cells present in the blastula. Thus in a one-half or a one-quarter embryo, while the number of cells in the blastula is not as great as the number in the normal blastula, the actual number of cells that is invaginated tends to equal the number invaginated in the whole embryo. In other words, it seems as though a definite number of cells were necessary for the formation of a given organ of the body. "I have been personally most loath," he adds, "to accept this conclusion, because it seemed a priori very improbable that a numerical question could enter into this problem, but I see no other alternative than to accept this view of the matter." It would seem that if this be the case in organ formation, the requirement is one rather of the number of cells entering into the composition of the organ, than a mere quantative regulation or partition of the amount of protoplasm.

The controversy over the relation between the cell size and body size may be taken too seriously. The writer has pointed out the various possible relations between body size and cell size. The problem does not involve a fundamental conception under which all data must be subsumed and made to agree. Different groups of animals may vary widely in respect to the possibility of a direct correlation between the two, the only problem of real concern is to what extent any given condition is fixed within a given group of organisms. In fact Morgulis ('11) has shown experimentally that the relation of cell size to body size may be altered in the individual through a change of physiological conditions. In connection with his observations on complete inanition he has said ('11, p. 259): "In the case of Diemyctylus it was found that the volume of both the cells and nuclei of different tissues diminishes

as the animal becomes smaller, and that with a return to normal diet, when the animal grows very rapidly, its cells again increase in volume.''

2. The beginning of constancy

Throughout the entire animal kingdom observations, chiefly incidental, have been recorded indicating that an organism or a single organ contains a fixed number of cells or of nuclei. Originally this condition was looked upon as of uncommon occurrence. Various workers among the protozoa have recorded the tendency for a single individual during sporulation or colony formation to give rise to a fixed number of cells. Thus in Tillina four spores are usually formed from a single individual, but this condition has not been absolutely fixed, for occasionally but two spores are produced. This would seem to indicate a transition from a reproduction by simple binary fission to a higher type where a larger number of individuals is produced from the parent cell. A step higher in the scale is Colpidium which, though normally producing four individuals in its temporary cyst, not infrequently forms eight. Among the colonial protozoa a single colony is frequently composed of a definite, constant number of cells: as an example of this Gonium pectorale might be cited. This is a sixteen cell colony in which each cell of the association in turn gives rise to a sixteen cell aggregate while still within the parent colony. In Eudorina is found an example where thirty-two undifferentiated cells arise from a parent cell producing a colony, as also in Pandorina which contains sixteen undifferentiated cells associated together. Thus in the protozoa there is a transition from the condition where reproduction is accomplished solely by simple binary fission, through a series of stages to that in which a definite number of cleavages result in the formation of a colony having a fixed number of individuals.

In the Metazoa, Conklin ('98) has distinguished a difference between the earlier and the later cleavages, attributing to the former the greater morphological importance:

The difference in the number of cells offers no difficulty in the doctrine of cell homology unless we assume that all divisions are differential, a thing which we know is not true. After blocking out the protoblasts of various regions and organs an indefinite number of non-differential divisions may occur either before or after the complete differentiation of the parts, and this probably explains the larger number of cells in the embryo of Crepidula adunca and the smaller number in the adult. In fact after the complete differentiation of all the tissues and organs, the number of cells may vary greatly in the different individuals of the same species or in the same individual at different times. In adult Crepidulas the number of cells varies directly as the body size varies, the cell size remaining practically constant. These later divisions, in the main, are non-differential, and likewise it is probable that in the later stages of cleavage many non-differential and inconstant divisions occur. Not only is there greater variation in the number and size of cells in later as compared with earlier stages of cleavage, but there is also greater variation in the direction and time of division; all of which goes to prove that the earlier cleavages are more constant, more frequently differential, and therefore morphologically more important.

In citing these instances wherein among the Protozoa and in the embryology of the Metazoa constancy seems to have a beginning I do not wish to give the impression that from such isolated and fragmentary citations I would claim to have traced a probable actual rise of fixity in numbers of cells going to make up an adult individual. In fact I do not consider cell constancy as of simple origin, for, while it occurs in broadly separated groups of the animal kingdom, it has probably arisen independently in each from the primitive, more variable conditions through the processes which tend toward the elimination of variability during the phylogeny of the group.

3. Factors involved in the production of cell constancy

For the explanation of the causes and limitations of cleavage various factors have been suggested. Reference has already been made to the works of Morgan as indicating that the production of the anlagen of organs in individuals developed from isolated blastomeres tends to require the same number of cells as required in normal development, even though the abnormal individuals are smaller than the normal and have fewer cells. Conklin's work has also been cited, wherein he considers the earlier cleavages

morphologically of more importance, while the later divisions in Crepidula are believed to be non-differential and inconstant, but so far no one has offered a satisfactory explanation of why this is true. I do not here attempt to suggest any new factors as determining the number and arrangement of the cleavages involved in organ formation, but from the facts observed in the development of colonial protozoa of constant numbers, and in the ontogeny of the metazoa where constancy has been demonstrated, there must be some inherent factor determining that a certain number of cell divisions shall precede the formation of a given organ, and that when this number is realized the power of further nuclear division becomes lost. Moreover evidence gained from the study of the members of the genus Eorhynchus tends to discredit the possibility of cell size acting as such a factor, for in case size determines the time when a cleavage or division takes place, cell division would continue throughout the life of the individual, since these worms continue to increase in size from the time they reach the final host until they are expelled from it. There must be some factor within the original cell which determines every cell division, from the first cleavage to the establishment of the final adult condition. Whether this determining element is a 'force' which becomes dissipated in the processes of cleavage so that, when the definitive number of cells has been attained, no further progress is possible on the account of the lack of this 'force,' or whether the cause is to be sought in the presence of definite substances within the cell in the nature of either 'determiners' regulating cleavage or materials that are used up in the processes of mitosis can not be decided in the present stage of knowledge of the subject.

4. Cytomorphosis

In the genus Eorhynchus is found an evident exception to the generally accepted view of cellular changes accompanying advance of age in animal tissues. Probably the most important point of difference, or at least the one most easily observed, is the fact that as soon as the animal has reached the point

of development when it has tak n on the body form of the adult, cell division either mitotic or amitotic, ceases to play any role whatever in the later history of the somatic cells. Among the numerous specimens of five species of this genus which I have examined there has not been, in any instance, the least indication of further increase in the number of cells constituting the body. This is evidenced by the entire lack of mitotic figures and also by actual count of the cells present. This gives good ground for doubting the generally accepted view that life must be accompanied by cell division as expressed in the contention that the cell has lost its lease on life as soon as it can no longer divide.

Nothing is known regarding the changes in Eorhynchus accompanying the differentiation of the embryonic cells into the tissues and organs of the adult, for no larval stages of any of the American species have been discovered, and none of the investigations upon the European species contain references to the changes in the structure of the cells at that time. In the later stages of development some slight changes have been observed in the structure of the nuclei but there are no strongly marked general cytological modifications such as usually accompany the advance of age. The nuclear change consists chiefly in the rearrangement of the chromatin. In the immature forms the nuclei, especially of the subcuticula and of the lemnisci, have their chromatic substance irregularly scattered throughout the nucleus, but with the advance to maturity this chromatic material assumes the form of a more compact solid mass lying in the center of the nucleus.

The conditions of existence for all of the cells of the body are so nearly uniform at all periods of life for the adult that it seems probable that death must follow as a consequence of the termination of the reproductive period of the individual or as the result of a combination of factors acting on the organism as a whole rather than as a gradual senescence of the individual cells.

5. Brief review of known extent of cell constancy in the animal kingdom

Lest the impression be conveyed that cell constancy is confined to occasional forms within a small group of animals the following condensed survey is given of the important work upon this topic. Martini has shown that constancy is present in most and probably in all of the organs of a new-born nematode. The muscle cells of Oxyurias are constant in number throughout life. Goldschmidt has demonstrated cell constancy in the nervous system of Ascaris. Brandes has found a definite number of brain cells in Gigantorhynchus, but has not pursued his studies to other organs of the body, nor has he deduced any general conclusions. Looss found constancy in the oesophagus of several nematodes. Apathy, working on the central nervous system of Hirudinea, emphasized the constancy found there. Hirschfelder found constancy in the midgut of Rotifera, while Martini following him has carefully worked out constancy in the entire body of Hydatina senta, so that he can recognize nine hundred and fifty nine individual cells, each of which he is able to locate in every of individual of that species. Woltereck has shown a constancy in the cells of the larva of Polygordius. Even in the Chordata constancy has been established by Martini in the various organs of Oikopleura, and Fritillaria. Aside from these definite records given as proofs of constancy by these writers, there exist masses of isolated facts such as have been cited in connection with the reviews of the work upon Acanthocephala in this article, but no attempt has been made to catalogue all of these scattered references. Miss Erdmann ('12) has given a very general survey of the literature upon cell constancy and the problems closely associated with it.

6. The significance of cell constancy

Cell constancy has a most interesting relationship to the problems of comparative anatomy and evolution. Evidently it can occur only in those forms which have a determinate cleavage. In what way has this condition been brought about? Were all forms of development originally of this type or has this condition been

developed only in certain groups of animals? If the latter be the case, then the question arises as to the factor or factors operating in widely separated groups, which could accomplish such an end. Up to the present time no direct attempt has been made to answer this question. There seems to have been a tendency, at least among some workers, to expect too great a future for the study of cell constancy. This has probably grown out of the failure to realize fully the limitations of the field. There is the possibility of a comparative anatomy, such as Martini has predicted, in which two forms may be compared one with the other in a much more intimate way than has been undertaken heretofore. In this case individual cells rather than gross anatomical structures would be used as units for comparison. An examination of the facts brought out in the earlier parts of this paper will show that they constitute just such a study in comparative anatomy. Necessarily such a study is limited to those groups which have acquired constancy.

The fact that cell constancy has never been demonstrated in any marked degree in organisms which hold an unquestioned position in the main line of descent of the animal series seems to indicate that it is not the primitive condition. The Nematodes, the Tunicates, the Rotifers, and the Acanthocephala, forms which most clearly display the phenomena of constancy, stand either as side branches from the main line of descent of animal life or as highly modified groups which have lost most of their indications of close relationship with other forms. For instance the rotifers have reached a point in development but little higher than the trochophore stage found in the development of higher forms and have become permanently fixed. The tunicates, coming off from the stem which has given rise to the Vertebrates, have, in a similar manner, either failed to proceed farther or, in case at one time they stood on a higher level, have through degeneration regressed to a condition where they have become fixed as an aberrant group. Parasitism has so profoundly affected the somatic portions of the Acanthocephala that little is left to serve as an indication of earlier phylogenetic relations. Especially, in this group, species and even genera differ from each other in slight

degree when compared with the range of variation in the more plastic groups of animals. This tendency toward uniformity of body characters has led to, or possibly has resulted from, a corresponding stability in the numbers of cells which go to make np the organs of the body in the genus Eorhynchus. It is true that within this genus the parasitic habit has contributed toward the elimination of physical factors which might induce radical changes. The result of this is that variability is practically confined to minor variations such as those of body size, and in general those which concern slight rearrangements of the component cells, rather than those involving the production of entirely new types of structures. The future of such a group of organisms is very clear. The stability which has been produced serves as an effective barrier to evolution. Under present conditions those organisms displaying marked cell constancy are incapable of producing new creations in the lines of organic progress, for the elimination of variability has precluded the possibility of progressive evolution.

I wish to express my indebtedness to Prof. H. B. Ward for the many helpful suggestions and kindly criticism of methods and of general outline of the work, rendered throughout the period of its preparation.

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ABBREVIATIONS

br., brain
bu., bursa
bw., body-wall
c., cuticula
cc., circular canals
cg., cement gland
ci., cirrus
cm., circular body muscles
cr., cement reservoir
fl., fan ligament
gg., genital ganglion
go., genital opening
ht., terminal hook
hb., basal hook
hm., middle hook
ip., proboscis invertor
l., *l.*2, lemnisci
loc., longitudinal canal
lm., longitudinal body muscle
ms., muscle sac
po., terminal proboscis organ
prn., nuclear ring of proboscis
r., receptacle of proboscis
s., subcuticula
sa., selective apparatus
sn., subcuticular nuclei
sr., sperm reservoir
ssa., stay of selective apparatus
ta., anterior testis
tp., posterior testis
u., uterus
v., vagina
vd., vas deferens
ve., vas efferens
vs., vaginal sphincter

EXPLANATION OF FIGURES

A camera lucida was used in making all the drawings included in the figures.

Figs. 1 to 16 Represent Eorhynchus gracilisentis (Van C.).

Fig. 1 Proboscis of hematoxylin-stained specimen in balsam. × 97.

Fig. 2 Hooks from the same specimen as shown in figure 1. × 310.

Fig. 3 Embryos from body of mature female. × 310.

Fig. 4 Portion of body wall showing a subcuticular nucleus. Sagittal section. × 310.

Fig. 5 Sagittal section to one side of that shown in figure 4, showing muscle nuclei. × 310.

Fig. 6 Sagittal section through proboscis showing terminal proboscis organ and hook retractors; hematoxylin. × 310.

Fig. 7 Sagittal section through proboscis receptacle of inverted specimen showing terminal organ of the proboscis. × 310.

Fig. 8 Sagittal section through base of proboscis receptacle showing location of brain. × 310.

Fig. 9 Cement gland of male; toto mount. × 97.

Fig. 10 Transverse section through tip of proboscis showing terminal ring of twelve nuclei. Iron hematoxylin. × 310.

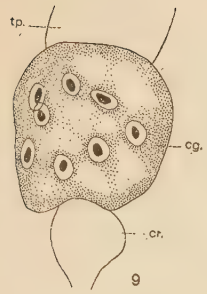
Figs. 11 and 12 Reconstructions of female genital tract. × 310.

Fig. 13 Female genital tract in toto mount; hematoxylin. × 310.

Fig. 14 Sagittal section of same, in region of vaginal sphincter. × 310.

Fig. 15 Fan-shaped ligament at side of female genital orifice. × 310.

Fig. 16 Retractors of the proboscis receptacle, from dissection. × 310.



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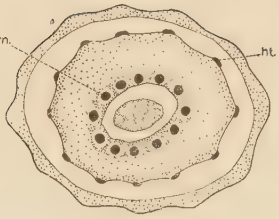

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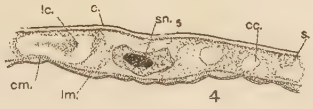

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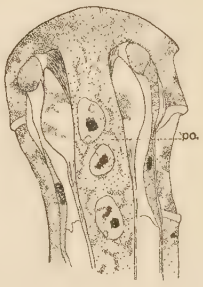

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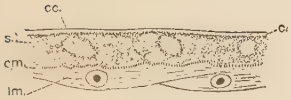

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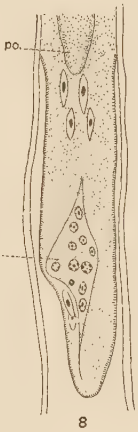

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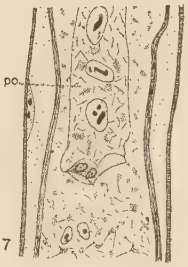

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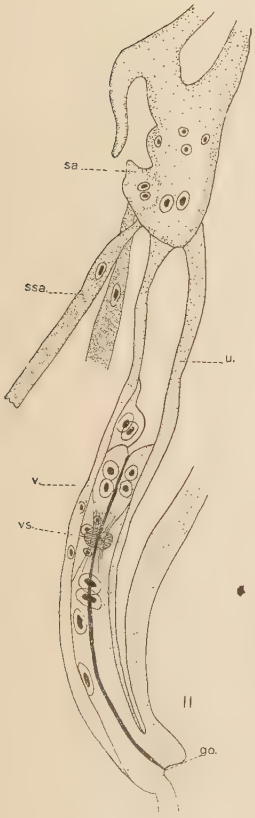

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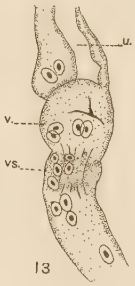

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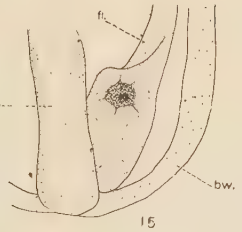

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Figs. 17 to 19 Eorhynchus gracilisentis. (Van C.).

Fig. 17 Genital organs in posterior region of male; reconstruction from sagittal sections.

Fig. 18 Reconstruction of male copulatory apparatus. × 310.

Fig. 19 Male copulatory apparatus everted; toto mount. × 97.

Figs. 20 to 28 Eorhynchus longirostris (Van C.).

Fig. 20 Cement gland. × 97.

Fig. 21 Proboscis of fully mature female; in balsam. × 97.

Fig. 22 Anterior end of body; proboscis retracted; toto mount. × 30.

Fig. 23 Portion of body wall in sagittal section. × 310.

Fig. 24 Embryos. × 310.

Fig. 25 Nuclei from muscle sac, posterior to cement reservoir. × 310.

Fig. 26 Sagittal section through anterior end of body, showing location of brain and terminal proboscis organ. × 97.

Fig. 27 Reconstruction of female genital tract, showing divisions and the nuclei. × 97.

Fig. 28 Dorsal retractor of proboscis receptacle; toto mount. × 97.

Fig. 29 Eorhynchus tenellus (Van C.), proboscis of mature male. × 97.

Fig. 30 Hooks of Eo. tenellus. × 310.

Fig. 31 Eorhynchus rutili; copied from Lühe, 1911. About × 20.

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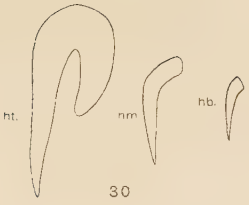
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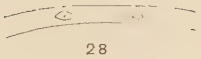
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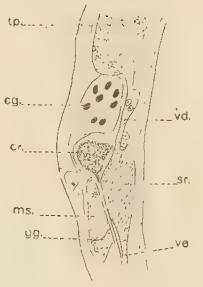
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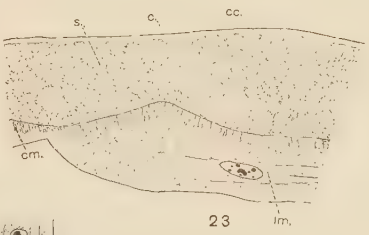
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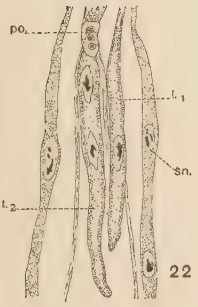
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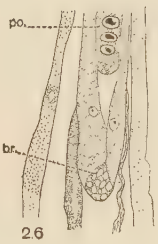
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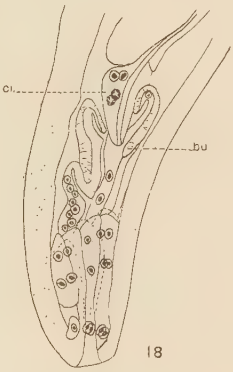
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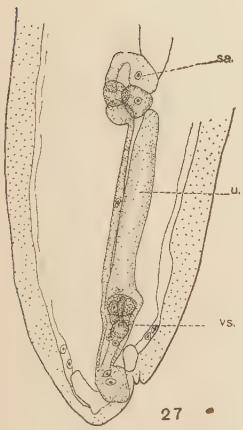
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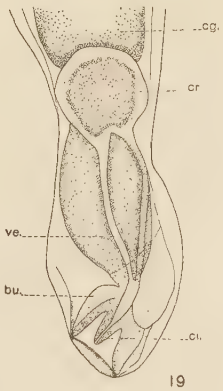
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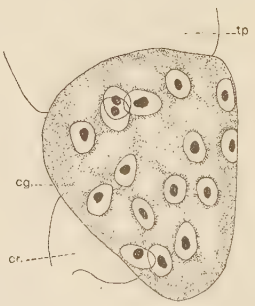
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Fig. 32 Eorhynchus emydis (Leidy); proboscis of fully mature female. × 97.
Fig. 33 Hooks of Eo. emydis. × 310.
Fig. 34 Embryos of Eo. emydis. × 310.
Fig. 35 Proboscis of Eo. cylindratus (Van C.) × 97.
Fig. 36 Hooks of Eo. cylindratus. × 310.
Fig. 37 Embryos of Eo. cylindratus. × 310.
Fig. 38 Eo. tenellus; reconstruction from sagittal sections of anterior end of body. × 97.
Fig. 39 Eo. tenellus; reconstruction of posterior end of female, showing genital tract. × 97.
Fig. 40 Eo. emydis (juv.); genital tract of female; toto mount. × 310.
Fig. 41 Eo. emydis; Cement gland of mature male. × 97.
Fig. 42 Eo. emydis; Cement gland of immature male. × 97.
Fig. 43 Eo. emydis (juv.); lemnisci in toto mount. × 97.
Fig. 44 Eo. emydis (juv.); proboscis receptacle and adjacent organs; toto mount stained in hematoxylin. × 97.
Fig. 45 Eo. agilis; longitudinal section, showing especially the terminal proboscis organ. Copied from Hamann, 1895, plate 3, figure 28.
Fig. 46 Eo. rutili; anterior end of body. Copied from Saefftigen, 1884, plate 5, figure 6.

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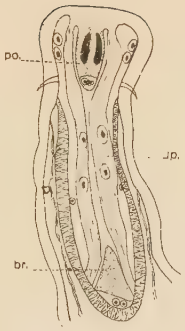

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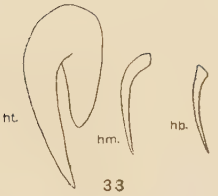

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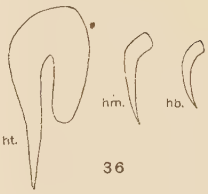

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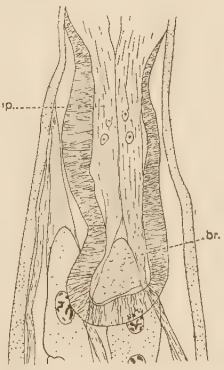

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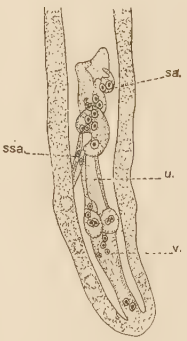

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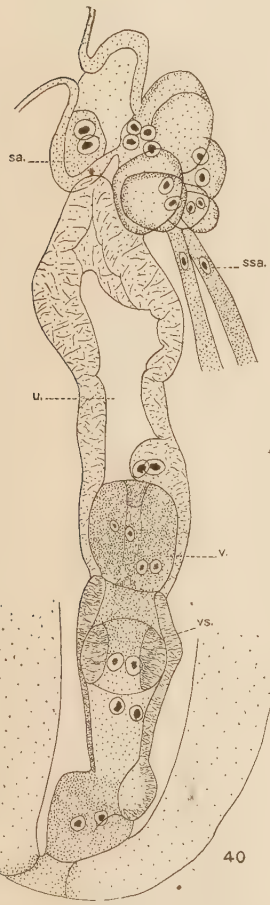

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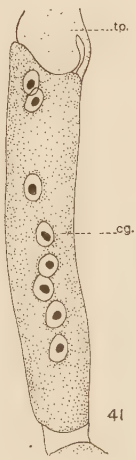

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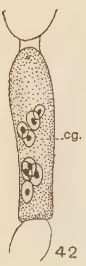

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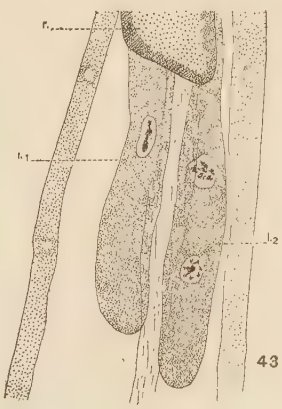

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VITA

Harley Jones Van Cleave was born October 5, 1886, at Knoxville, Illinois. He received his elementary education in the public schools of that city and was graduated from the High School in 1905. From 1905 to 1909 he was a student in Knox College, at Galesburg, Illinois. The last two years of that time he was Student Assistant in Biology. In 1909 he received the degree of Bachelor of Science. The summer of 1909 was spent in the Marine Biological Laboratory at South Harpswell, Maine. The four years immediately following he was enrolled in the Graduate School of the University of Illinois: 1909–1910 as a Scholar in Zoology, receiving the M.S. in 1910; the summer of 1910 as an Assistant in Zoology in the Illinois Fresh Water Biological Station; 1910–1911 as a Fellow in Zoology; 1911–1912 as an Assistant in Zoology; and 1912–1913 as Head Assistant in Zoology. He was elected to membership in the Society of Sigma Xi in 1910.